Biology of *Thrypticus truncatus* and *Thrypticus sagittatus* (Diptera: Dolichopodidae), Petiole Miners of Water Hyacinth, in Argentina, with Morphological Descriptions of Larvae and Pupae

M. CRISTINA HERNÁNDEZ[1]

USDA–ARS—SABCL, South American Biological Control Laboratory (B1686EFA), Hurlingham, Buenos Aires, Argentina

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ABSTRACT The mining flies *Thrypticus truncatus* Bickel & Hernández and *Thrypticus sagittatus* Bickel & Hernández (Diptera: Dolichopodidae) are being evaluated as biological control agents for the water hyacinth, *Eichhornia crassipes* (Martius) Solms-Laubach (Pontederiaceae). The behavior of adults and larvae of these species was studied in the laboratory and in several water courses of the Paraná River basin, Argentina. The larvae feed on sap from feeding points scraped in the vascular bundles in the petioles of *E. crassipes*. Pupation occurs in a chamber dug near one of the mine's openings. External morphology of larvae and pupae, larval cephalic skeleton, and tracheal system are described. The pupae of both species have the ventrally flattened profile of the Medeterinae, with a transverse serrate ridge divided by a notch at the apex of the head. The mines, described herein in detail, constitute the microhabitat where the larvae live throughout their development, and obtain food and protection. Both species are active and reproduce on water hyacinth from spring to the end of fall, and overwinter as larvae inside the mines in the petioles. No morphological or behavioral differences were evident between the immature stages of these species, except in the apical ridges of the pupae. Both species seem to occupy the same niche on the plants.

RESUMEN Las moscas minadoras *Thrypticus truncatus* Bickel & Hernández y *Thrypticus sagittatus* Bickel & Hernández (Diptera: Dolichopodidae) están siendo evaluadas como agentes para el control biológico de la maleza acuática *Eichhornia crassipes* (Martius) Solms-Laubach (Pontederiaceae). Se realizaron observaciones de comportamiento de adultos y larvas de estas especies, en laboratorio y en diversos cuerpos de agua de la cuenca del Río Paraná, en Argentina. Las larvas se alimentan de savia a partir de orificios de alimentación roídos en los haces vasculares de los pecíolos de *E. crassipes*. Ellas desarrollan toda su vida dentro de la mina hasta empupar en una cámara construida en un extremo de la misma. Se describen la morfología externa de larvas y pupas, el esqueleto cefálico y el sistema traqueal de las larvas. Las pupas poseen el perfil plano de las Medeterinae, con una estructura serrada dividida por una hendidura transversal en el ápex de la cabeza. Se describe la estructura de la mina, la que constituye el micro hábitat donde las larvas obtienen alimento y protección. Ambas especies están activas y se reproducen sobre *E. crassipes* desde primavera hasta fin del otoño y sobreviven durante invierno como larvas dentro de los pecíolos de *E. crassipes*. No se encontraron diferencias morfológicas ni de comportamiento entre las larvas de ambas especies, excepto en el serrado apical de las pupas. Ambas especies parecen ocupar el mismo nicho sobre la planta.

KEY WORDS larval morphology, larval behavior, sap feeders, larvae, pupae

The genus *Thrypticus* Gerstäcker (Medeterinae: Dolichopodidae) is widely distributed all over the world, with some 94 described species (Grichanov 2008). All of the known larvae that have been studied have phytophagous habits. However, the majority of the adults and larvae in the family Dolichopodidae, with some 259 genera and ≈7,186 species (Grichanov 2008), are predacious on small, soft-bodied arthropods, including Homoptera, Collembola, Psocoptera, Thysanoptera, eriophyid mites, annelids, cladocerans, Odonata eggs, bark beetle, and early instar caterpillars (Ulrich 2005).

Thrypticus is closely related to *Corindia* Bickel and *Medetera* Fischer. Nothing is known about the immature stages of *Corindia*, but it is possible that their larvae develop in the subcortical environment of trees, similarly to *Medetera* larvae, which are free living and predatory (Bickel 1986, Dyte 1993).

[1] Corresponding author, e-mail: crisher@speedy.com.ar.

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Several species of *Thrypticus* have been reared from monocot hosts. *Thrypticus fraterculus* Wheeler was found in stems of *Scirpus acutus* Muhl. ex Bigel. (Cyperaceae) (Green 1954). In the Poaceae, *Thrypticus muhlenbergiae* Johannsen & Crosby was obtained from *Muhlenbergiae sylvatica* Torr. ex Gray (Johannsen and Crosby 1913); *Thrypticus smaragdinus* Gerst. from *Phragmites australis* (Cav.) Trin. ex Steudel (Luben 1908); and *Thrypticus violaceus* Van Duzee from *Spartina alternifolia* Loisel (Strong 1984). In Pontederiaceae, *Thrypticus truncatus* Bickel & Hernández, *Thrypticus sagittatus* Bickel & Hernández, *Thrypticus yanayacu* Bickel & Hernández, *Thrypticus chanophallus* Bickel & Hernández, and *Thrypticus circularis* Bickel & Hernández all were reared from the water hyacinth, *Eichhornia crassipes* (Mart.) Solms-Laubach; *Thrypticus azuricola* Bickel & Hernández and *Thrypticus romus* Bickel & Hernández from *Eichhornia azurea* (Swartz) Kunth; *Thrypticus formosensis* Bickel & Hernández from *Pontederia cordata* L.; and *Thrypticus taragui* Bickel & Hernández, from *Pontederia subovata* (Seub.) Lowden (Bickel and Hernández 2004, Hernández 2007).

Thrypticus larvae have morphological differences with the other dolichopod larvae. In 20 genera of the Dolichopodidae, the larvae have four terminal lobes (Dyte 1967). The lobes are surrounding the posterior spiracles and are only absent in a few species, e.g., *Medetera signaticornis* Loew (Medeterinae) has the last segment rounded, and *Neurigona* sp. (Neurigoninae) has one medial lobe under the posterior spiracles (Krivosheina 1960).

Thrypticus lacks the four large terminal lobes. *T. muhlenbergiae* and *T. fraterculus* have larvae with a rounded last segment (Johannsen and Crosby 1913, Green 1954).

The head skeleton in Dolichopodidae has two types: the *Liancalus*-type, common to the predaceus larvae; and the *Thrypticus*-type, found only in phytophagous larvae (De Meijere 1916, 1947; Vaillant 1948; Dyte 1967). The figures in De Meijere (1916, 1947) indicate that the head skeleton in the larvae of *Thrypticus* differs considerably from the *Liancalus* type.

The pupae in the Dolichopodidae have two distinctive sutures on the ventral side of the head. These sutures run downward from the cephalic apex to behind the base of the antenna on each side (Dyte 1967). *Thrypticus* pupae have pointed spiracles on the second to fifth abdominal segments in addition to the prothoracic respiratory horns seen in other dolichopodids (Hinton 1953).

The mining fly *Thrypticus* sp. was recognized as a potential biocontrol agent of water hyacinth since early surveys during the 1960s. Bennett and Zwölfer (1968) first mentioned *Thrypticus*, probably *Thrypticus minutus* Parent (Bennett, unpublished data; Dyte 1993), attacking water hyacinth in northern South America and Trinidad. They described and illustrated the damage and estimated insect density, but they did not give information on the host specificity. In the 1970s, Cruttwell (1973) reported preliminary investigations on the life history of an unidentified *Thrypticus* species associated with water hyacinth. Field explorations carried out by staff of the South American Biological Control Laboratory (SABCL) in Argentina, from 1997 to 1999, showed that *Thrypticus* spp. attacked every common species in the Pontederiaceae (Cordo et al. 2000). Further research revealed that there was a complex of nine sibling species using the Pontederiaceae, which was later enveloped in the *truncatus* species group of *Thrypticus*. The larvae of four of them, *T. truncatus*, *T. sagittatus*, *T. yanayacu* and *T. chanophallus*, breed in the basal part of the long petioles of water hyacinth; and *T. circularis* larvae mine exclusively in the bulbous form of petioles. The species *T. truncatus*, *T. sagittatus* and *T. circularis* were found in the Paraná-Paraguay rivers basin, which comprises northeastern Argentina, southeastern Brazil, and eastern Paraguay. In addition, *T. truncatus*, *T. circularis*, *T. yanayacu*, and *T. chanophallus* were collected in the upper Amazon, near Iquitos, Peru (Bickel and Hernández 2004).

According to the taxonomic results, preliminary observations and tests, *T. truncatus* was selected as a candidate for the biocontrol of water hyacinth. *T. sagittatus*, however, did not reproduce well in rearing cages, so fewer studies were devoted to this species.

Bionomic information of adults, feeding behavior and morphological aspects of the immature stages of *T. truncatus* and *T. sagittatus* are presented here. In addition, the mine characteristics are described as part of the larval habitat.

Materials and Methods

Flies and Plant Sources. *Thrypticus* larvae were collected primarily from two main sites: Carabelas Grande River in the Paraná delta, Buenos Aires Province (34° 4′98″ S, 58° 48′6″ W); and Palo Santo, Formosa Province (25° 33′25″ S, 59°19′35″ W), both in the Paraguay-Paraná rivers basin of eastern Argentina. Petioles of water hyacinth infested with *Thrypticus* larvae were gathered from the field, and the basal 30 cm, where the mines are located, were incubated at room temperature in opaque bottles with a transparent vial in the cap. The emergent flies were collected from the vials and kept on a cold dish to identify the species and sex. To obtain a culture, adults of the same species were released on a mat of water hyacinth, cultivated in a canvass pool (2 by 1.4 by 0.6 m) enclosed in 6.5-m^3 walk-in cages. Originally, all plants were collected as small plants in the field and cultivated, free of *Thrypticus*, in pools with water with the standard dose of nutrients used by Satô and Kondo (1981).

General Behavior of Adults. Most of the observations were carried out on infested water hyacinth in these walk-in-cages. For more detailed observations small cages with one or two plants were used. In some cases, the pupae were incubated in a rearing chamber at 25°C, in complete or sectioned petioles, to identify the species of the emerging adults and to correlate them with the mines shapes.

Feeding Habits of Larvae. The mines used for the descriptions were gathered from a *T. truncatus* culture on water hyacinth petioles, and slices containing one mine were cut. The habits of the larvae of different ages, to feed and to tunnel, were observed dissecting the mines carefully under dissecting microscope. To verify that the larvae feed on sap, a trial with water hyacinth with colored sap was performed with *T. truncatus* larvae. Petioles with larvae were cut 8 cm above the mines level, and the petiole section was covered immediately with cotton wool soaked in a water solution of red food dye (pigments: Red *punzó* 4R and dioxide of titanium). The color went down by the vascular bundles, probably due to the interruption of the natural circulation of the sap both in xylem and phloem. Three hours later, the mines were dissected to observe whether the larvae had red dye in their guts.

Morphology. Specimens of all stages of *Thrypticus* spp. were observed with both dissecting and compound microscopes. No special entomological techniques were necessary for the observations of the tracheal system or the internal organs because of the transparent larval cuticle. To observe the head skeletons the entire larvae were immersed in a 10% sodium hydroxide solution for 2 min. The external morphology was observed and photographed with an environmental scanner electronic microscope. The terminology used follows Vaillant (1948), Robinson and Vockeroth (1981), and Sinclair (1992).

Reproductive Period. The oviposition period under natural conditions was studied in a canal (200 by 10 m) connected to the Carabelas Grande River, in the temperate climate region of this basin. A water hyacinth mat covered the whole canal and supported a natural population of *T. truncatus* and *T. sagittatus.* Five sites were marked 15 m apart along the canal. At each site, a tagged, noninfested water hyacinth plant was inserted in the local plant mat for 15 d to expose it to *Thrypticus* oviposition. After this period the plants were taken to the laboratory to record the presence of mines. The mines found were expressed as mean number of mines per plant. This trial was carried out eight times from March 2001 to February 2002. No statistical analysis were performed because the low number of replications.

Results

General Behavior of Adults

Thrypticus truncatus and *T. sagittatus* are small flies (1.5 mm body length), with metallic bluish green body. They thrive in the protected microenvironment under the water hyacinth canopy, which was found with specificity test to be their sole host (M.C.H., unpublished). These flies are very elusive insects. The individuals remain on the basal part of the petioles, making short flights up and down or between the petioles. They walk backwards down the petiole toward the water surface. The adults eclose around noon. In the laboratory, *T. truncatus* adults live for ≈5–9 d, and it takes ≈45 d for their complete development (egg to adult).

Eclosion begins with upward waving movements of the body inside the pupal chamber (see Pupae). These movements allow them to tear the coating of the pupal chamber, and to lift the operculum with the apex of the head of the pupal exuvia. At the same time, the movements of the body cleave the pupal cuticle along the sagittal line of the head, freeing the adult, that leaves the pupal cuticle adhered to the exit hole. The process continues with the extension of the legs and the expansion of the wings. Finally, the fly rests until the full expansion and sclerotization of the cuticle are completed.

It is possible that the adults obtain food and water from the surface of the petioles because they were observed touching the surface with their mouthparts. They also drink descending by the petiole to the water level.

Courtship and Mating

Usually, the individuals remain in the middle part of the water hyacinth petioles with their heads upwards. Before mating, the male moves toward the female and jumps repeatedly over her from front to back. In some of these jumps, he rests for an instant on the female; if the female remains still, the mating takes place in the next jump. The male introduces the hypandrium together with the aedeagus into the female genital atrium. The hypandrium acts as a guide for the aedeagus and may enter the female before the aedeagus. During the coupling the cerci and surstyli reach the third abdominal sclerite of the female, where they touch the abdomen rhythmically. The copula lasts 1–2 min and takes place during the warmer part of the day. One female followed since eclosion was observed to mate 6 h after emergence and to mate six times within ≈2.5 h.

Oviposition and Eggs

The eggs of *Thrypticus* spp. have not been found on the plant, despite exhaustive examination under a dissecting microscope. However, the females exhibit a recurrent behavior that could be interpreted as the oviposition sequence. The female moves up from the basal part of the petiole touching the surface with the aculeus of the oviscapt and jumps down on the petiole; periodically, it stops and bends the abdomen, it is assumed that this constitutes oviposition. The shape of the oviscapt, and the dorso-ventral movements of the aculeus, suggest that the egg is inserted into the petiole. The egg may be laid in the basal part of the petiole, just beyond the leaf sheath. However, it is frequent to find mines under the leaf sheaths, where it seems impossible for the female to lay the eggs. It seems that the newly emerged larva moves downward through the aerenchyma, crossing the horizontal diaphragms. This migration leaves a very small hole in each diaphragm, which can be detected by a pale brown tone in the tissues. The eggs of *T. truncatus*,

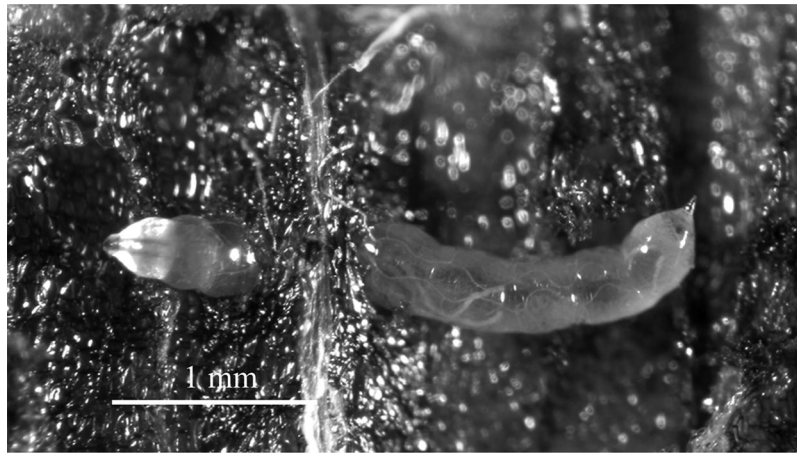


Fig. 1. *T. truncatus* larva inside a mine partially dissected, in a water hyacinth petiole.

obtained by dissection of the female, are whitish, cylindrical and slightly curved, with one rounded and one acute extreme (0.45 by 0.02 mm).

Morphology of Immature Stages

Larvae. The larvae of *T. truncatus* and *T. sagittatus* have no evident morphological differences, show similar feeding behavior, and were both reared from *E. crassipes.* The following descriptions correspond to the full grown larvae.

External Morphology. Body slender, subcylindrical, slightly compressed dorso-ventrally. Cuticle thin and translucent; crystalline grayish white body contents (Fig. 1). The head segment is movable and retractile. Mandibular hooks protrude from the mouth downwards, whereas the hook and cones of the labrum do so upward (Fig. 2). At each side of the oral opening there is a bristle inserted in the connecting sclerite of mandible, sensu Sinclair (1992); more ventrally are a maxillary sensorial complex (mc) and an antennal complex (ac). The ac has several small cylindrical structures, which can be seen through the transparent cuticle, and a bigger structure with rounded apex that stand out in the surface. In addition, small papillae can be seen with the compound microscope at the sides of the head. Each thoracic segment bears a cluster of four hairs latero-ventrally (Fig. 2). The anterior-ventral margin of the abdominal segments has a creeping welt covered with minute spinules (Fig. 3 and 4). The contractions of the muscle in each segment of the body form a lateral lobe at each side. The last segment is rounded, with a conical projection (Fig. 5), and ventrally it has a round anal pad with a longitudinal slit (Fig. 6). The larvae do not have spiracles.

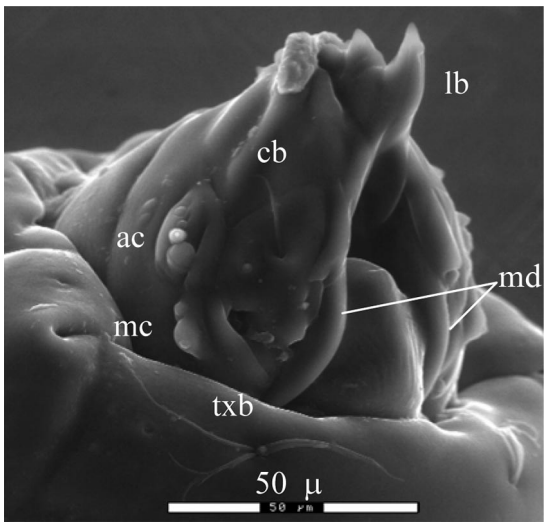
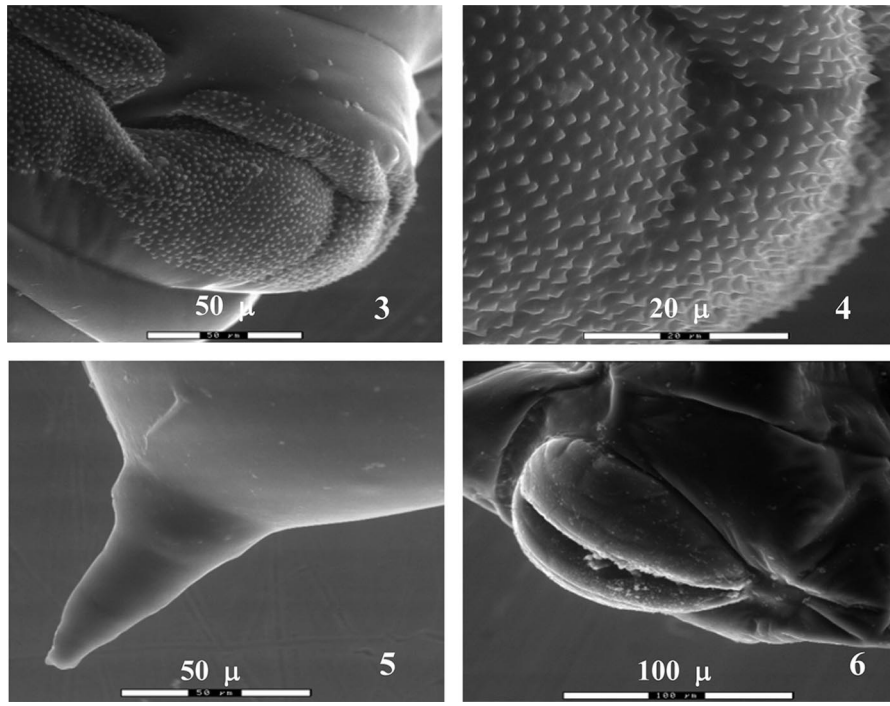


Fig. 2. *T. truncatus,* larval head segment, latero-ventral. ac, antennal complex. cb, connecting sclerite bristle. lb, labrum hook. mc, maxillary sensorial complex. md, mandibular hook. txb, toraxic bristles cluster.

Cephalic Skeleton. In both species the cephalic skeleton is brown and is the only colored structure in the larval body. The labrum and the mandibular hooks can be seen from the exterior.

The labrum has a strong upwards hook, slightly curved backward, followed by a medial conical projection and four posterior smaller projections (Fig. 7). The mandibles have a hook, strong and curved backward, and a small projection toward the base of the hook; they are articulated through a series of sclerites to the tentorial bars, and dorsally to the sclerites that form the cephalic capsule. The labium on the ventral side of the mouth cavity, not visible from the outside, has short conical projections bent backwards. These, together with labrum, are probably used to scrape the plant tissues. The labium articulates backward with the hypopharynx, a V-shaped sclerite. The pharyngeal sclerite is extended behind it and between the tentorial bars. The tentorial bars are expanded posteriorly, characteristic of the dolichopodids, and the metacephalic bars are straight and parallel. All the cephalic skeleton sclerites are joined in an ovoid structure, probably muscular, that constitute a mobile, solid unit (Fig. 8). The labrum and the mandibular hooks can



Figs. 3–6. *T. truncatus* larva. (3) Creeping welt in abdominal segment, ventral. (4) Spinules of the creeping welt. (5) Conical projection in the last segment. (6) Anal pad, ventro-lateral.

move up and down, either together or independently of each other. These three hooks are almost constantly in movement and they serve to tear the plant tissues up. In the rest position, the tips of the three hooks are joined.

Tracheal System. This system comprises two dorsal trunks running along the body (Fig. 8); the anterior part of each dorsal trunk is branched out into numerous tracheoles toward the cephalic segment. Toward the rear there are nine dorsal transverse commissures joining the dorsal trunks. There are lateral branches extending downward intercalated between the dorsal commissures. Each of these trunks is divided, with one branch forward and one backward; the branch pointing backward is joined with the forward branch from the next segment composing a lateral tracheal trunk. Each dorsal trachea in the seventh segment is divided in several small branches and one of them is curved forward, and runs to the midsection of the body. Both *T. truncatus* and *T. sagittatus* larvae are apneustic.

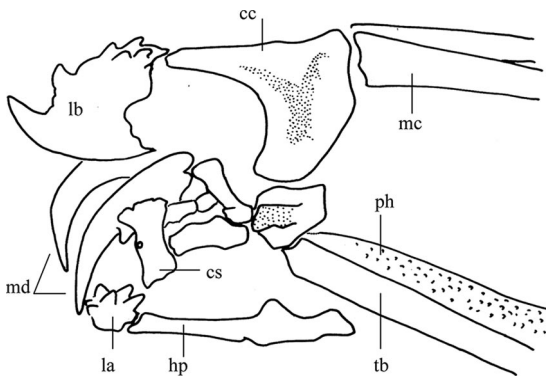


Fig. 7. *T. truncatus*, cephalic skeleton of full grown larva, left lateral. cc, cephalic capsule. cs, connecting sclerite. hp, hypopharynx. ph, pharynx. la, labium. lb, labrum. mc, metacephalic bar. md, mandibular hook. tb, tentorial bar.

Pupae. Before pupating, the full grown larva digs a chamber at one end of the mine and cuts an operculum in the petiole epidermis. It then seals the interior of the chamber with a translucent film and rests there folded in two until the pupation process. After 11 d (25°C), the adult emerges.

The pupae in both species of *Thrypticus* are ventrally flattened (Fig. 9), and this is possibly characteristic of the Medeterinae as some *Medetera* species also show ventral flattening. The apex of the head has a transverse serrated ridge divided by a notch at the top (Fig. 10, n). These apical ridges are slightly different in the two species. In *T. truncatus* the serration is more jagged, with bigger tooth, than in *T. sagittatus*, and the notch is slightly wider in *T. sagittatus* than in *truncatus.* The head has a pair of short and strong setae on the dorsum and another pair near the antennal tubercles on the ventral side. The pupae have a pair of sutures running together from the apical cephalic tubercle and diverging to behind the antenna as in Fig. 10, s. There are respiratory horns at the sides of the prothorax, and on the second to fifth abdominal segments (Fig. 9).

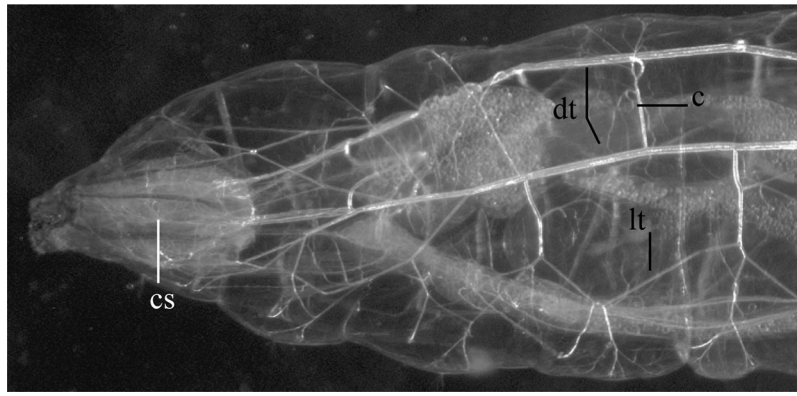


Fig. 8. *T. truncatus* larva, tracheal system in the forepart of the body. Dorso-lateral view. c, commissure between dorsal trunks. cs, cephalic structure. dt, dorsal trunk. lt, lateral trunk.

Mine Characteristics and Feeding Habits

The mine is transverse with respect to the water hyacinth petiole. The larva goes through the aerenchyma cells finding the vascular bundles and scraping a small portion on each, the feeding orifice. At each feeding point, the larva moves forward crossing through one of the lateral walls of the vascular bundle until it finds other vascular bundles (Fig. 11). When the larva reaches the epidermis, it makes an orifice, such that the mines have an opening at each end. Thus, a *Thrypticus* tunnel is constituted by consecutives cells connected by the holes dug in the aerenchyma walls. The larva supports its body on several of these septa simultaneously, except when it changes its advance direction; at that point, it introduces the whole body in the last cell and goes back. The openings in the walls are always equal to the diameter of the larval body (Fig. 11). The larvae never go out of the mine. The trace of the mines is not regular, being either branched or not, and it shows no distinctive pattern for either species. Initially, the tunnel lacks an outside connection, and the air from the aerenchyma cells is sufficient for the young larva. Water never enters in the tunnel if the tissue is healthy, but if water inundates the mine, the larva dies.

Although the larva eats the tissues to dig the mine, it feeds mainly on the sap that exudes from the damaged bundles in the feeding points. In the trial carried out with colored sap, the larvae showed red color in their guts 3 h after the coloration of the sap. Yeast were found related with the larval body, which suggests that the nourishment could be supplemented by these yeast (Hernández et al. 2007).

Mortality Factors

Microbial diseases or drowning by mine flooding were observed. Neither parasitoids nor predators have

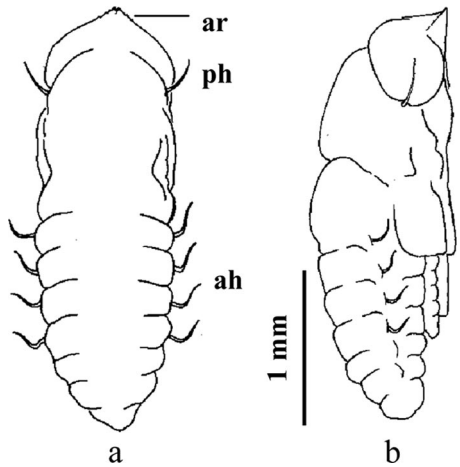


Fig. 9. *T. truncatus* pupa. (a) Dorsal. (b) Lateral. ah, abdominal respiratory horn. ar, apical ridge. ph, prothoraxic respiratory horn.

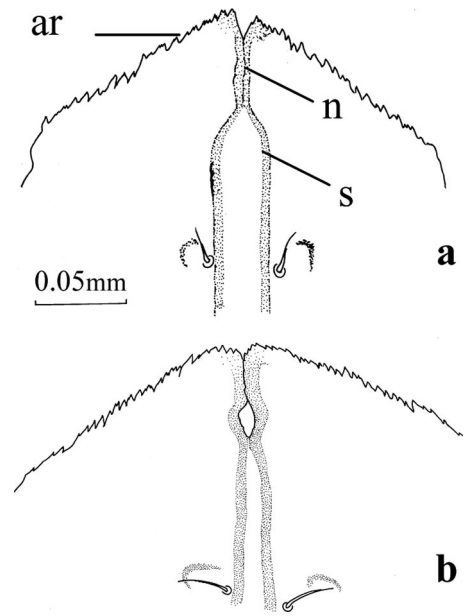


Fig. 10. Apex of the pupa, ventral. (a) *T. truncatus.* (b) *T. sagittatus.* ar, apical ridge. n, notch. s, ventral suture.

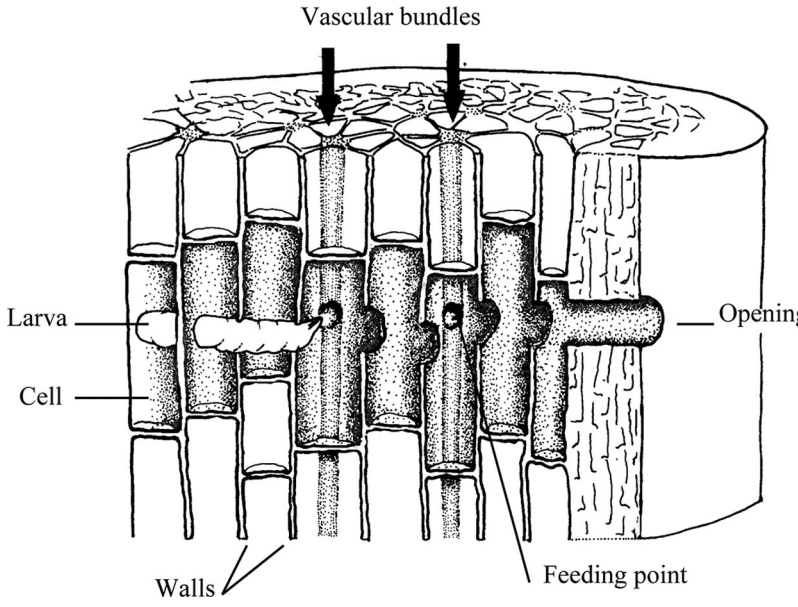


Fig. 11. Mine scheme of *T. truncatus* and *T. sagittatus*.

been found for any stages, but some larval cannibalism was observed when the mines were confluent.

Reproductive Period

The oviposition period recorded finished at the beginning of fall, and no mines were obtained in the plants exposed in the coldest part of the winter. At the latitude of the Paraná delta, the winter frosts damage the upper part of the water hyacinth plants, but the basal part of the petioles, were the larvae are located, remain green. No adults were observed during this period, and no pupal opercula were found. Consequently, *T. truncatus* and *T. sagittatus* overwinter as larvae in the basal part of the petioles of water hyacinth. Reproductive activity started again in the spring, toward the second half of September, with the emergence of a first cohort of adults. Mines were obtained throughout the warm season, with a maximum mean number of mines per plant at the end of January (Fig. 12). In spite of the low number of observations recorded, the description of the activity along the seasons was quite similar to those reported by Poi de Neiff and Casco (2003). They worked in a warmer site located also on the Paraná basin but 1,000 km north of the delta site. They recorded the number of mines of an unidentified species of *Thrypticus* in samples of water hyacinth over several seasons. The abundance of mines was high in spring and at the end of summer with a minimum during a short period in winter.

Laboratory cultures of *T. truncatus* were established in discrete generations. The adults released to establish a culture survived 7–10 d, after that the colony comprised the offspring larvae for a month until a new adult generation emerged.

Discussion

Thrypticus is a genus with phytophagous habits in a predominately predacious family. In addition, they have developed a very special larval feeding habit as sap feeders. The species *T. truncatus* and *T. sagittatus*, which belong to *truncatus* group, use the microenvironment inside the aerenchyma of water hyacinth to develop the immature stages. This behavior provides them habitat, nutrition, and protection from predators and parasitoids. Both species seem to have the same niche, developing enclosed in the aerenchyma; however, more specific research is necessary to know whether they have overlapped niches and whether competition occurs. Immature stages show only slight

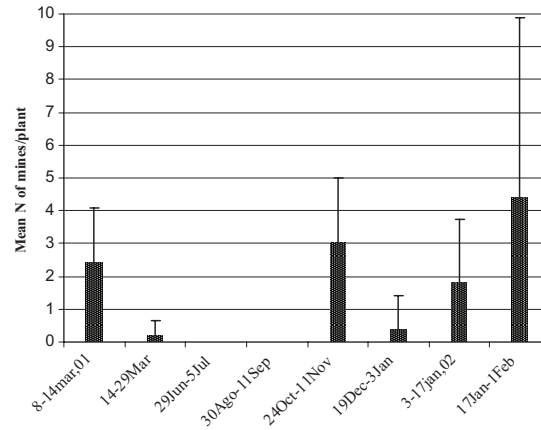


Fig. 12. Reproductive period of *T. truncatus* and *T. sagittatus* populations on *E. crassipes* (2001–2002), in the lower Paraná Rv. delta, Argentina.

morphological or behavioral differences, but adults of these two species have distinct morphological differences that allow them to be readily separate (Bickel and Hernández 2004).

The species of the *truncatus* group develop in species of *Eichhornia* and *Pontederia* and all of them tunnel mines similar to those of *T. truncatus* and *T. sagittatus* (Hernández 2007). The genitalia is distinctive for this group, and together with the specialized way of life of the larvae, make them an interesting phylogenetic subject of study.

The bionomic aspects found in *Thrypticus truncatus* and *T. sagittatus* are good attributes for a candidate of biocontrol because ensure a strong association with the host, and the tests to establish their specificity on water hyacinth, currently under development, seem to confirm it. The last aspect under investigation is regarding whether they produce damage on the host. Besides the effect that the sap feeding would produce on the plants, *Thrypticus* have and indirect effect because the mines are the habitat for 31 fungal species, some of them known pathogens on water hyacinth (Hernández et al. 2007).

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